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Ecosystem Engineers, Ants and Termites

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Ecosystem engineers (EE) are organisms that directly or indirectly modulate the availability of resources to other species by causing durable changes in biotic or abiotic materials [7]. In so doing, they physically modify, maintain, or create habitats. Among the social insects, ants and termites present the most notable examples of builder organisms. They are active agents in the cycling of plant and animal nutrients and in the structuring of tropical soils and stand out as the most capable of causing durable physical changes in the environment that significantly modulate resources and habitat for other species, thereby affecting their life histories.

Ecosystem engineering is seen as an important paradigm of contemporary ecology. The idea that components of the biota can modulate the availability and flow of matter to the benefit of other species or the overall health of the environment is used to explain phenomena in the most varied ecosystems. Indeed, as emphasized by the concept proponents, it is unlikely that there exists in the biosphere any ecosystem that is not dependent or has not previously been dependent, in one way or another, on the activities of engineer organisms.

The physical state changes introduced by EEs directly create nonfood resources such as living space, while directly controlling abiotic resources and indirectly modulating abiotic forces that, in turn, affect resource use by other organisms [8]. Although most of these phenomena were long known in ecology, the concept of ecosystem engineering has the merit of drawing attention to their ubiquity and importance, providing an integrative general framework to their understanding toward an integrated framework that exposes the essential cause/effect relationships, their underpinnings, and the interconnections that need to be understood to explain or predict ecosystem engineering effects.

Two basic types of EEs are recognized. *Autogenic engineers* (e.g., corals and trees) change the environment via their own physical structures as living and dead tissues, while *allogenic engineers* (e.g., termites, ants, and beavers) institute changes by transforming living or nonliving materials from one physical state to another by mechanical or other means [7]. While autogenic structures are physical manifestations of living organisms in the abiotic environment, allogenic structures are formed by the engineers in the abiotic environment from nonliving or living materials, such as

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suspended soils and the dam in tank bromeliads. Many mobile animals are obvious allogenic engineers, while many sessile organisms are obvious autogenic engineers. However, engineers can be mobile and autogenic (e.g., shells of some living mollusks can create epibiont habitat), sessile and allogenic (e.g., plant root growth creates soil macropores), and simultaneously auto- and allogenic (e.g., many plants, microbial soil surface crusts).

As noted, an EE's impact is often greater when modulated resources are used by many other species or when it modulates abiotic forces affecting more than one species. Basically, six factors dependent on the space-time scales shape an EE's impact [7]: (i) lifetime per capita activity of the individual engineering organisms; (ii) population density; (iii) spatial distribution of the population, both locally and regionally; (iv) length of time that the population has been present in one place; (v) type and formation rate of the constructions, artifacts, or impacts, and their durability in the absence of the original engineers; and (vi) quantity and types of resources that are modulated by constructions and artifacts, and the number of other species dependent on these flows.

Social Insects

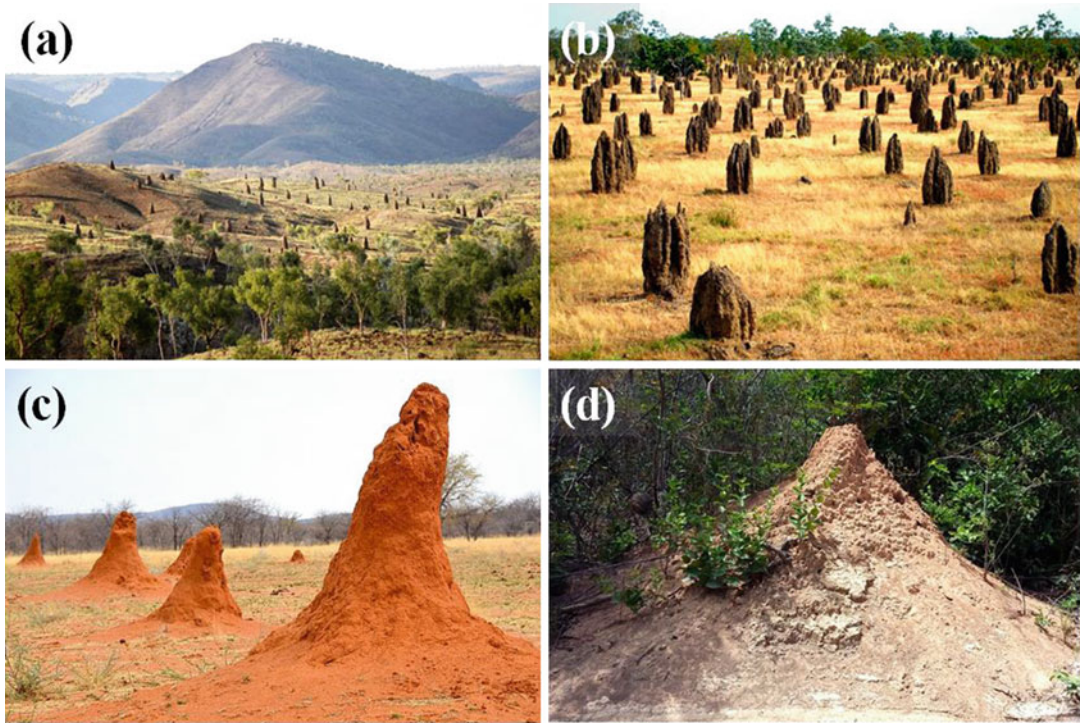
Social insects present many of the most outstanding examples of builder organisms to be found in nature. Among these, ants and termites as active agents in the cycling of plant and animal nutrients and modifying the structure of tropical soils, stand out as the most capable of causing large, long-standing physical changes in the environment. Both leave constructs with impacts that extend many lifetimes beyond their own (e.g., large mound nests of termites in savannas around the World and underground "ant cities" in tropical rainforests – Fig. 1). These structures, whether above or below ground, can have ecosystem-level effects that may last for many years, even centuries.

Quite apart from their sheer numbers, biological characteristics of social insects have a strong influence on their roles and impact as EEs. Group integration and division of labor favor the successful development of colonies and consequently their persistence in one place, so that flourishing colonies of some groups can be seen to occupy the same site over long periods. Group integration and division of labor are also essential in allowing colonies to make complex structures that may remain long after the colony, itself, has disappeared. Such structures significantly modulate resources for other species.

Ants and termites are important allogenic engineers in all tropical and subtropical environments, where they are involved in key processes of ecosystem functioning and dynamics, such as organic matter decomposition, nutrient cycling, stimulation of microbial activity, and soil bioturbation. Paleontological records of burrowing, including well preserved ichnofossil nests of termites in paleosols suggests that at least these insects were key geomorphologic engineers since the early Triassic through soil mixing, gas and water exchange dynamics, as well as organic material cycling [6].

Some ants and termites have a substantial impact on pedogenesis, soil properties and functions, so that are important mediators of soil ecological processes [1, 4, 9, 10]. From their activities in long time scales, they modify the soil's hydraulic properties and temperature and improve the aeration, retention, and water infiltration capacity. They can also promote soil stability and water permeability, while modifying soil chemistry. Large nest densities of the same species of ants (e.g., mounds of *Lasius flavus*, *Camponotus mus*, members of the *Formica rufa* group, refuse and tunnels of *Acromyrmex balzani*, etc.) or termites (e.g., *Macrotermes* mounds in Africa and Asia) can also cause physicochemical or structural alterations of the vegetation, the leaf-litter or superficial mineral soil. Furthermore, termites through their microorganismic gut symbionts degrade and utilize even the most recalcitrant residues of dead plant material, such as lignin, cellulose, and humus.

Termites have the ability to modulate the flow of resources to other organisms (e.g., plants and microorganisms) through the collection and processing of plant material and by the manipulation

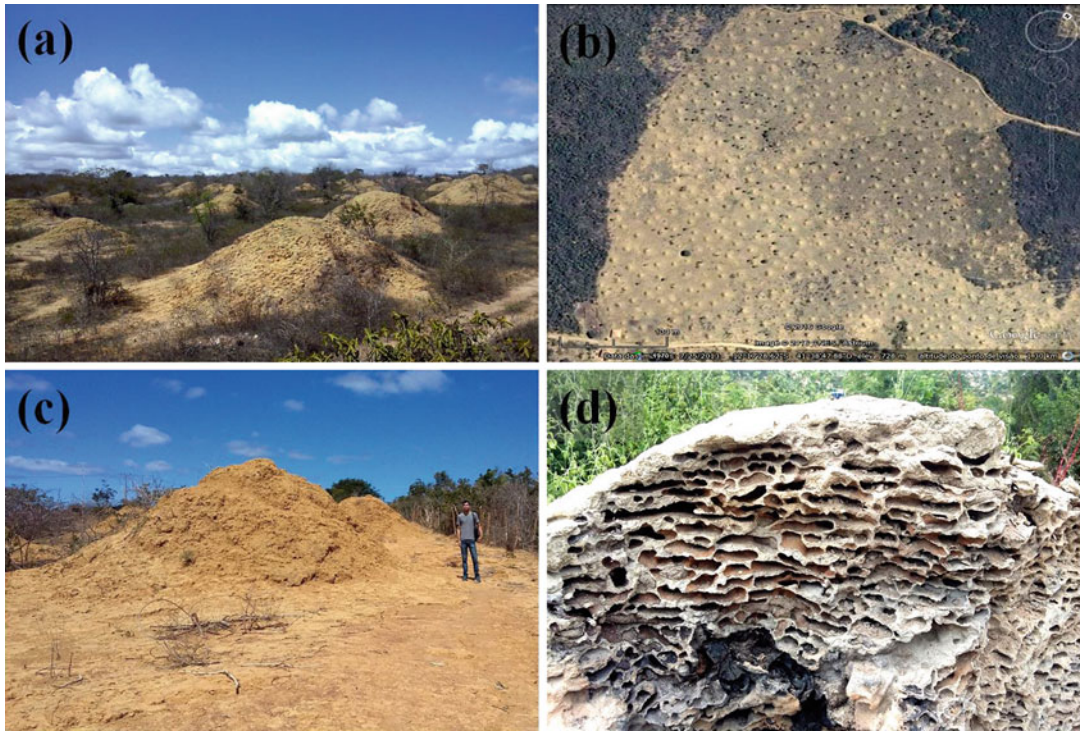


Ecosystem Engineers, Ants and Termites, Fig. 1 Termite mounds around the world. (**a**) Bungle Bungle Range in Western Australia; (**b**) Matilda Highway in Queensland, Australia; (**c**) Namibia in Africa; (**d**) *Syntermes dirus* nest in Northeast region of Brazil. Images "**a**–**c**" are licensed under the Creative Commons "Attribution Non-commercial." Image "**d**" was taken in the State of Bahia, Brazil

and translocation of soil particles to build nests and galleries. Thus, they are considered EE primarily because of their ability to physically modify the environment. These structures generally consist of organomineral aggregates with specific physicochemical properties, depending on the builder species and the soil where the activities are developed [3]. Such structures are highly diverse and widely distributed both above and below soil and can be regarded as micro-sites where macroscale ecosystem processes are regulated.

The production of biogenic structures impacts several processes in the soil and affects the availability and distribution of resources to other organisms. A notable example is the influence of termite mounds on the distribution and abundance of the vegetation on African savannas [5, 12, 13]. Termites accumulate carbon, phosphorus, and nitrogen in the mound soil and in so doing influence the dynamics of organic matter and the release of available minerals to plants. For this reason, ecologists usually consider the termite-built biostructures as nutrient hotspots, sometimes referred to as "fertility islands" that influence savanna ecosystem processes at various spatial and temporal scales.

The tunneling activity of many ants and termites favors the creation of pores in the soil that increase gas exchange, water infiltration, nutrient movement, root penetration, and the movement of other soil organisms. Tunneling also promotes the mixing of soil and creation of aggregates that influence both its fertility and the spatial distribution of nutrients. For example, the content of C, N, and P in termite mounds is generally associated with organic matter incorporation by workers, as leaf-litter particles and fecal pellets mixed with saliva. When feeding, the termites break down the plant matter vegetal into minute particles, facilitating the action of fungi and soil bacteria that favor the formation of high-fertility humic substances, which are displaced upwards during the building process.



Ecosystem Engineers, Ants and Termites, Fig. 2 *Murundus* in the semiarid region of Brazil. (**a**) Densely packed *murundus* in the *Caatinga* (seasonally dry tropical forest) vegetation during the dry season; (**b**) Google Earth's satellite images showing densely packed *murundus* clearly evident in areas deforested; (**c**) earth mound *murundu* during the dry season, showing their conical shape; and (**d**) preserved galleries built by termites in the middle-upper portion (up to 90 cm depth) of one *murundu*. Images "**a**, **c**, and **d**" was taken during the dry season in a densely packed *murundus* in the State of Bahia, Brazil

Termites are able to build specialized nests with a regulated warm and moist internal environment. They conserve metabolic heat by building with insulating materials, constructing ventilation shafts to circulate air, and transporting water from the groundwater to humidify the nest and foraging areas. Furthermore, under certain circumstances, termite engineers can also transfer heat to soils via convection, a process that may have important consequences for microbial activity in mound soils and may at least partially explain the often increased rates of nutrient cycling observed in mounds relative to surrounding soils.

Each ant or termite nest represents a large investment by the colony. However, many other organisms benefit from this investment by exploiting these constructs, including vertebrates and invertebrates and a variety of microorganisms. In active termite nests – in particular among the most common organisms that benefit from the structure of the nest – are the ants and beetles, especially those belonging to the family Staphylinidae, but also spiders, cockroaches, isopods, among others. The presence of termite species other than the one that constructed the nest structure is also frequently observed.

Once the ant and termite nests are abandoned, they can be home to an even greater number of small animals. For example, nests of *Nasutitermes* sp. in their original arboreal position have been found to serve as nest sites for birds or bats. Abandoned nests of *Atta* and termites are used by burrowing owls for nesting.

Considering that the greater impact of ecosystem engineer is attributable to species with large per capita effects, living in high densities over large areas and for a long time, giving rise to structures that persist for centuries and affect

many resource streams [7], termite savannas in Africa and the *murundus* structures in the semi-arid region of Brazil are some of the most notable examples of ecosystem engineering by social insects. Termite mounds are a widespread feature in most African savannas. They exhibit high nutrient contents and often host a typical floristic composition and vegetation patterning induced directly or indirectly through the termites' foraging activities, associated nutrient cycling, and their interaction with mammalian herbivores or fire [13]. The fungus-growing Macrotermitinae play an especially prominent role from the modification of local water infiltration rates to the creation of regional landscape mosaics [2]. They enhance decomposition processes and alter nutrient content, texture, and hydrological properties of soils through their foraging and building activities. The mounds of *Macrotermes* species supply a critical resource of scarce micronutrients to wildlife and vegetation [12].

In South America, *murundus* are earth mounds that exhibit a wide range of sizes and convexity but generally have a hemispherical to conical shape and average 1.5–3 m in height and 8–20 m in diameter at the base, correspond to a soil volume of up to 600 m^3 for a single structure (Fig. 2). Recently, evidences obtained from predictive, spatially explicit modeling and physical-chemical soil analyzes have suggested a termite origin for these structures from convergent observations: (i) there is a strong geographic congruence between the distributions of densely packed *murundus* and four mound-building termite species (*Cornitermes bequaerti*, *C. silvestrii*, *Syntermes dirus*, and *S. wheeleri*), suggesting that the formation of those structures is an adaptive response of mound-building termites to particular environmental conditions [14]; (ii) the regular pattern distribution and density of *murundus* within densely packed areas suggest the action of an important scale-dependent feedback with characteristics similar to competition for foraging territories between different colonies during the formation of their structures [15]; and (iii) physical (clay texture), chemical (high nutrient content), and biological (galleries, tunnels, and royal chambers) traces of termite construction show that *murundus* were not only occupied by those insects but also built-up by them [16].

There are thousands of mounds ranging in age from 690 to 3,820 years [11] over an area of 230,000 km^2 corresponding to 27% of the *Caatinga* biome and equivalent to about the size of Great Britain. The geographical dominance of *murundus* is now considered one of the greatest examples of ecosystem engineering produced by nonhuman animals [14].

References

1. Bignell, D. E. (2006). Termites as soil engineers and soil processors. In H. Konig & A. Varma (Eds.), *Soil biology* (Vol. 6, pp. 183–220). Berlin: Springer.
2. Dangerfield, J. M., McCarthy, T. S., & Ellery, W. N. (1998). The mound-building termite *Macrotermes michaelseni* as an ecosystem engineer. *Journal of Tropical Ecology, 14*, 507–520.
3. Decaëns, T., Galvis, J. H., & Amézquita, E. (2001). Properties of the structures created by ecosystem engineers at the soil surface of a Colombian savanna. *Comptes Rendus de l'Académie des Sciences – Series III, 324*, 465–478.
4. Frouz, J., Jílková, V., & Sorvari, J. (2016). Contribution of wood ants to nutrient cycling and ecosystem function. In J. A. Stockan & E. J. H. Robinson (Eds.), *Wood ant ecology and conservation* (pp. 207–220). Cambridge: Cambridge University Press.
5. Gosling, C. M., Cromsigt, J. P. G. M., Mpanza, N., & Olff, H. (2012). Effects of erosion from mounds of different termite genera on distinct functional grassland types in an African savannah. *Ecosystems, 15*, 128–139.
6. Hasiotis, S. T. (2003). Complex ichnofossils of solitary and social soil organisms: Understanding their evolution and roles in terrestrial paleoecosystems. *Palaeogeography, Palaeoclimatology, Palaeoecology, 192*, 259–320.
7. Jones, C. G., Lawton, J. H., & Shachak, M. (1994). Organisms as ecosystem engineers. *Oikos, 69*, 373–386.
8. Jones, C. G., Lawton, J. H., & Shachak, M. (1997). Positive and negative effects of organisms as physical ecosystem engineers. *Ecology, 78*, 1946–1957.
9. Jouquet, P., Traore, S., Choosai, C., Hartmann, C., & Bignell, D. (2011). Influence of termites on ecosystem functioning. Ecosystem services provided by termites. *European Journal of Soil Biology, 47*, 215–222.
10. Lavelle, P., Bignell, D., & Lepage, M. (1997). Soil function in a changing world: The role of invertebrate ecosystems engineers. *European Journal of Soil Biology, 33*, 159–193.

11. Martin, S. J., Funch, R. R., Hanson, P. R., & Eun--Hye, Y. (2018). A vast 4,000-year-old spatial pattern of termite mounds. *Current Biology, 28*, R1283–R1295.
12. Moe, S. R., Mobaek, R., & Narmo, A. K. (2009). Mound building termites contribute to savanna vegetation heterogeneity. *Plant Ecology, 202*, 31–40.
13. Sileshi, G. W., Arshad, M. A., Konaté, S., & Nkunika, P. O. Y. (2010). Termite-induced heterogeneity in African savanna vegetation: Mechanisms and patterns. *Journal of Vegetation Science, 21*, 923–937.
14. Souza, H. J., & Delabie, J. H. C. (2016). 'Murundus' structures in the semi-arid region of Brazil: Testing their geographical congruence with mound-building termites (Blattodea: Termitoidea: Termitidae). *Annales de la Société Entomologique de France, 52*, 369–385.
15. Souza, H. J., & Delabie, J. H. C. (2017). Fine-scale spatial distribution of *murundus* structures in the semi-arid region of Brazil. *Austral Ecology, 43*, 268–279.
16. Souza, H. J. (2017). *A Origem dos Murundus no Semiárido Brasileiro* [The origin of *murundus* in the semi-arid region of Brazil]. PhD Thesis. Universidade Federal da Bahia, Salvador, Brazil.